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BEHAVIORAL MEANS OF COEXISTING IN OLD FIELDS BY HETEROSPECIFIC ARTHROPOD PREDATORS (ARANEAE: LYCOSIDAE, SALTICIDAE; INSECTA: COLEOPTERA, CARABIDAE)

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Abstract.—Behavior is an important factor affecting competitive and predatory interactions among species. We investigated how the behavior of common arthropod predators in old-fields may affect coexistence of this diverse group of organisms. Through pitfall trapping, we found that different taxonomic groups varied their peak activities, possibly to avoid activities of other species. However, the major determinant of activity level appeared to be size, not taxonomic affiliation. Small predators, which are more vulnerable to intraguild predation, were most active when larger predators were not. Field experiments on some of the more common species (the lycosid spiders *Rabidosa rabida, R. punctulata,* Salticid spiders, and the omnivorous beetle *Harpalus* sp.) indicated that arthropod emigration rates were affected by the presence of other species. Potentially competing species had higher emigration rates when placed in plots together. When smaller predators, that could also be potential prey, were placed with larger predators, the larger predators reduced their emigration rates, because the increase in availability of food (i.e., the smaller predators) apparently outweighed any competitive effect between species. These experiments indicate that behavior can be an important component of predatory interactions. We suggest that behavioral adjustments can facilitate coexistence of predatory species, and are especially important in arthropod communities in which numerous species have overlapping resource use.

Key Words: Lycosidae, Carabidae, predation, behavior, niche partitioning

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We hypothesized that one way by which species avoid competitive or predatory exclusion is to vary their temporal use of habitat. We also hypothesized that species could alter their behaviors depending on the presence of potential competitors and predators. We tested these hypotheses first by trapping arthropod ground predators during 24-hour periods to determine their peak activity times. Second, we performed manipulative field and laboratory experiments to examine behavioral responses and potential interactions of several common groups of predators.

There has been increasing focus on the role of behavior in determining the outcome of interactions between species. Behavioral changes (such as foraging patterns or timing of activity) may be in response to competition (Jones et al. 1988, Werner 1992), predation risk (Sih 1987, Lima and Dill 1990, Moran and Hurd 1994, Moran et al. 1996, Schmitz et al. 1997, Schmitz 1998, Rangeley and Kramer 1998), and food level (Moran and Hurd 1997). These behavioral responses, that include changes in spatial and temporal use of habitat, prey choice, and activity level, may ultimately influence ecosystem characteristics by affecting trophic level processes (Moran et al. 1996, Schmitz et al. 1997) and species coexistence (Polis and McCormick 1987).

Arthropod predators constitute a particularly diverse group of organisms in early successional communities (e.g., old-fields). Cursorial spiders are often abundant (Cherrett 1964, Hagstrum 1970, Riechert and Bishop 1990) and can have significant impacts on prey species (Oraze and Grigarick 1989, Riechert and Bishop 1990, Fagan and Hurd 1991). They also form a diverse assemblage with up to 20 species in old-fields (Hurd and Fagan 1992). Other potentially important ground predators include ants, beetles (especially Carabidae and Staphylinidae), scorpions, and centipedes. Almost all species from these groups are generalist predators and therefore feed on a variety of prey, including each other (i.e., engage in intraguild predation, Polis et al. 1989). An important question is how does this diverse species assemblage coexist while seeming to exhibit large amounts of niche overlap?

MATERIALS AND METHODS

The study site is a level 10 hectare field in Faulkner Co., Arkansas, on the Hendrix College campus. The college mows it once per year in late autumn to prevent its succession to forest. Common plants include *Solidago* sp., *Smilax* sp., *Rosa multiflora* Thunb, *Rudbekia hirta* L., and *Poa* sp. The arthropod assemblage is diverse with numerous representatives of Araneae and the insect orders Homoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, Coleoptera, and Lepidoptera.

To determine activity patterns of the arthropod ground predators during the autumn, we performed pitfall trapping during 24-hour periods. Eighty pitfall cups, 3 cm in diameter and 6.5 cm deep, were placed in a straight north-south line 0.5 meters apart with the tops flush to the ground. Traps were placed in the center of the field to reduce edge effects from surrounding forest. During trapping periods, the cups were filled with isopropyl alcohol to a depth of 5 cm. Traps were sampled every four hours beginning at 08:00 giving 6 periods during a given 24-hour period.

Captured arthropods were stored in 95% ethanol, sorted, classified, and measured. Pitfall trapping was performed four times: 9, 25, and 30 Sept., and 15 Oct. 1997. We trapped only on days that had clear skies and when ambient temperatures did not drop below 10°C. Effects of time periods on activity were analyzed by one-way ANOVA followed by a least significant difference (LSD) post-hoc test. Data that violated the homogeneity of variance assumption were $\log_{10}$-transformed prior to analysis.

We then performed two field experiments testing short-term behavioral interactions between common species from the pitfall trap experiment. We chose those species captured most often in our pitfall traps since these are likely to have the strongest interactions. Plots were 0.25 m^2 (0.5 m × 0.5 m) and constructed of 15-cm high angle iron with an 8-cm wide lip. The plots were buried approximately 2 cm into the ground to prevent the movement of focal arthropods under the plots. The lip of the angle iron was painted with a layer of Tangletrap (Tanglefoot Co., Grand Rapids, MI) to monitor the movement of arthropods out of the plots. Because of the small plot size, experiments were performed for 5-day periods.

For each field experiment, there were 30 plots. Since each experiment involved the interaction between two species, the treatments consisted of 1) species 1 alone, 2) species 2 alone, and 3) species 1 and 2 together. Treatments were systematically interspersed within the plot array (Hurlbert 1984).

The most commonly captured predatory arthropods in the pitfall experiment were the spiders *Rabidosa rabida* Walckanaer, *R. punctulata* Hentz, and numerous species of Salticid spiders (jumping spiders) from the genera *Metaphidippus* Cambridge, and *Phidippus* Koch. We used *R. rabida* and *R.*

punctulata interchangeably in field experiments since they are closely related and very similar in size (15–20 mm in body length) and behavior (Kaston 1948, Brady and McKinley 1994). The omnivorous carabid beetle *Harpalus* sp. Latreille, which feeds on seeds and small arthropods, was also numerous, being the most common arthropod captured. Individuals were between 9–13 mm in body length.

The first experiment was designed to test the interactions between the two cursorial spiders *Rabidosa rabida* and *R. punctulata,* and the omnivorous carabid beetle *Harpalus* sp. Treatments consisted of 1) 5 *Rabidosa* sp., 2) 5 *Harpalus* sp., and 3) 5 of each species with ten replicates of each treatment. For 5 days after introduction, the Tangletrap barriers were monitored daily to record emigration of the manipulated species.

The second field experiment was similar in design, but tested the interaction between *R. rabida* and *R. punctulata* and salticid spiders (jumping spiders). The salticids were in the genera *Metaphidippus* and *Phidippus;* all were small species less than 5.0 mm in body length. Treatments consisted of 1) 4 *R. rabida* only, 2) 10 salticids only, and 3) 4 *R. rabida* and 10 Salticids together. The experiment was also conducted for 5 days during which emigration was monitored daily. Since these experiments used small numbers of organisms, we utilized a Mann-Whitney U-test to detect significant treatment effects.

To test potential predatory interactions in the field, we performed two laboratory experiment in plastic enclosures 11 cm in diameter and 7 cm deep (approximately 500 ml). In experiment 1, we placed one *R. rabida* or *R. punctulata* with a *Harpalus* sp. In experiment 2, we placed *R. rabida* or *R. punctulata* with one salticid without the addition of any other prey. We performed 10 replicates for each experiment. Individuals were randomly assigned to containers and used only once. We placed a small amount of leaf litter in each container and misted each with distilled water daily to provide suitable habitat. Observations before the experiments showed that these species would feed and survive in these conditions for a minimum of 2 weeks. Individuals were left in containers for 5 days and these were monitored daily to determine if any predation had occurred. Although this was a highly artificial environment that certainly increased the probability of interaction, we were concerned only with determining if predation was possible between the pairs of species.

RESULTS

Three groups of arthropod predators were fairly common in our 24-hour samples: carabid beetles (mostly *Harpalus* sp., an omnivorous species) and salticid and lycosid spiders. We therefore plotted daily activity patterns for these groups. The most commonly captured spiders were the large spiders, *Rabidosa rabida,* and *R. punctulata.* Others included small species of Lycosidae and small numbers of spiders from the families Oxyopidae, Amaurobiidae, Linyphidiae, and Thomisidae. There was no clear trend for activity of lycosid spiders, with activity occurring almost any time of the day (Fig. 1A), and no significant effect of time period on number of spiders captured ($F_{5,18} = 2.00$, $P = 0.127$). The activity of the ground beetles (*Harpalus* sp.) was significantly affected by time period (log transformed data, $F_{5,18} = 0.465$, $P = 0.017$), with most activity occurring during the morning from 08:00 through 12:00 (Fig. 1B). Some were captured during all periods, but 51% were captured during this one 4-hour period in the morning. Activity of salticid spiders showed a significant peak activity time in the early morning ($F_{5,18} = 2.82$, $P = 0.047$) from 04:00 through 08:00 with 59% captured during this period (Fig. 1C).

We also plotted the spider activity patterns according to size. Spiders less than 5.0 mm body length had low activity during most time periods and significantly higher

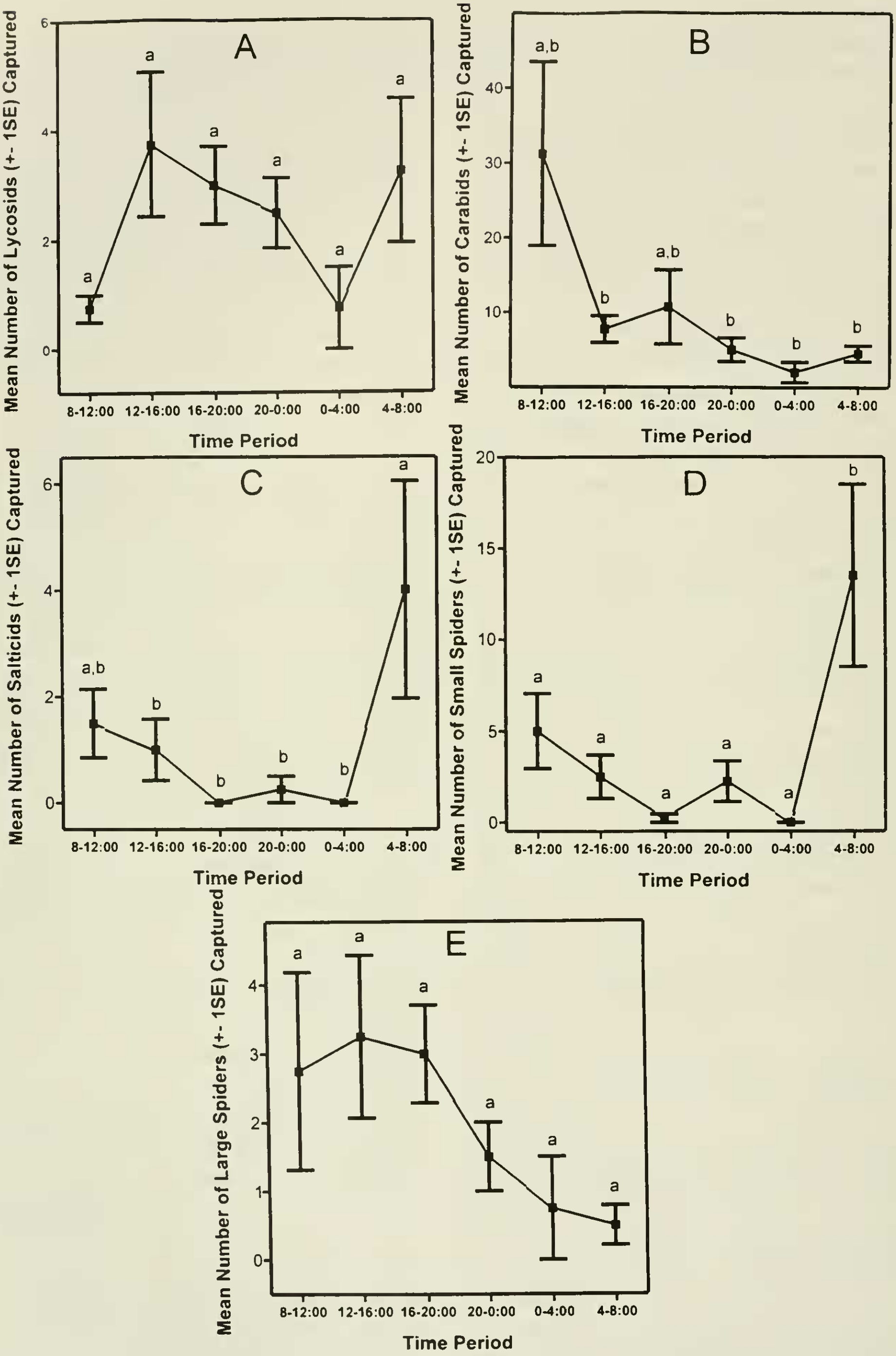

Fig. 1. Daily activity patterns. A, Lycosid spiders. B, Omnivorous carabid beetles. C, Salticid spiders. D, Cursorial spiders less than 5.0 mm in body length. E, Cursorial spiders greater than 5.0 mm in body length. Data are mean number captured (±1SE) in pitfall traps during four 24-hour collection trials. Letters above means indicate different subgroups (LSD post hoc analysis).

activity during the 04:00 through 08:00 period when 57% were captured (log transformed data, $F_{5,18} = 9.66$, $P < 0.001$, Fig. 1D). Time period had no significant effect on spiders greater than 5.0 mm body length ($F_{5,18} = 1.77$, $P = 0.169$), although there was a trend for more activity over a long period from 08:00 through 20:00, and somewhat lower activity at night (Fig. 1E).

In field experiment 1 which paired *Harpalus* sp. and *Rabidosa* spp., the emigration of *Rabidosa* spp. was significantly greater when *Harpalus* sp. was present (Mann-Whitney U = 24.00, $P = 0.03$, N = 20, Fig. 2A). *Harpalus* sp. can fly, so we captured none on the emigration barriers. We, therefore, used pitfall trapping and hand searching to capture those that remained in the plots at the end of the experiment to enumerate those that did not emigrate. When *Rabidosa* spp. were present, there were significantly fewer *Harpalus* remaining in the plots (Mann-Whitney U = 23.00, $P = 0.04$, N = 20, Fig. 2B). In the laboratory, *Harpalus* sp. and *Rabidosa* pp. appeared to have little ability to prey on each other, even under the artificial conditions in our small containers. Of the 10 pairings, one *Harpalus* sp. and one *Rabidosa* sp. died and were partially eaten after 5 days. However, in 80% of the pairings, both individuals were still alive after 5 days.

In field experiment 2, which paired *Rabidosa* spp. with small salticid spiders, the emigration of *Rabidosa* was significantly reduced when salticids were present (Mann-Whitney U = 7.00, $P = 0.001$, N = 20, Fig. 2C). The emigration of salticids was not affected by the presence of *Rabidosa* spp. (Mann-Whitney U = 38.50, $P = 0.37$, N = 20, Fig. 2D). In the 10 laboratory pairings, all salticids (100%) were consumed by *Rabidosa* spp. in less than 24 hours, showing that they can readily feed on small salticids.

DISCUSSION

Although most arthropod predators exhibited some activity during all time periods, there were peak activity times for most groups. These peak activity times seemed to correlate with low activity patterns for some potential competitors or predators. For instance the peak activity of carabid beetles (08:00–12:00 hours) was one of the lower activity periods for lycosids. The field experiment showed that the lycosid spiders (*R. rabida* and *R. punctulata*) and carabids changed their emigration rates in response to each other. This does not necessarily mean that they change their temporal habitat use, but simply show that these two species can respond to each other. Since they do not appear to prey on each other, the response is probably competition for food, space, or both. The peak activity time of carabids during the low activity of lycosids may represent attempts of potential competitors to avoid each other.

Peak activity of salticids was early in the morning, but this was a time when lycosids were also active. However, most of the large lycosids capable of preying on salticids (i.e., those lycosids larger than 5.0 mm in body length) were active during later periods (from 12:00–00:00). The large number of small spiders active from 04:00 to 08:00 hours included many smaller lycosid species, some juveniles of larger species, as well as most of the salticids. Therefore, body size seemed to be a more important predictor of activity pattern then taxonomic affiliation.

Most generalist predators take prey based on size, not taxonomic classification. Therefore, intraguild predation is common among these groups (Polis et al. 1989, Hurd and Eisenberg 1990, Snyder and Hurd 1995), with larger predators feeding readily on smaller predators. While several studies have shown that the threat of predation affects the spatial use of habitat (Stamps 1983, Moran and Hurd 1994, Moran et al. 1996, Lima and Dill 1990, Anholt and Werner 1995, Schmitz et al. 1997), our study also points to the possible effects of predation risk on temporal use of habitat (Polis and McCormick 1987). The activity pat-

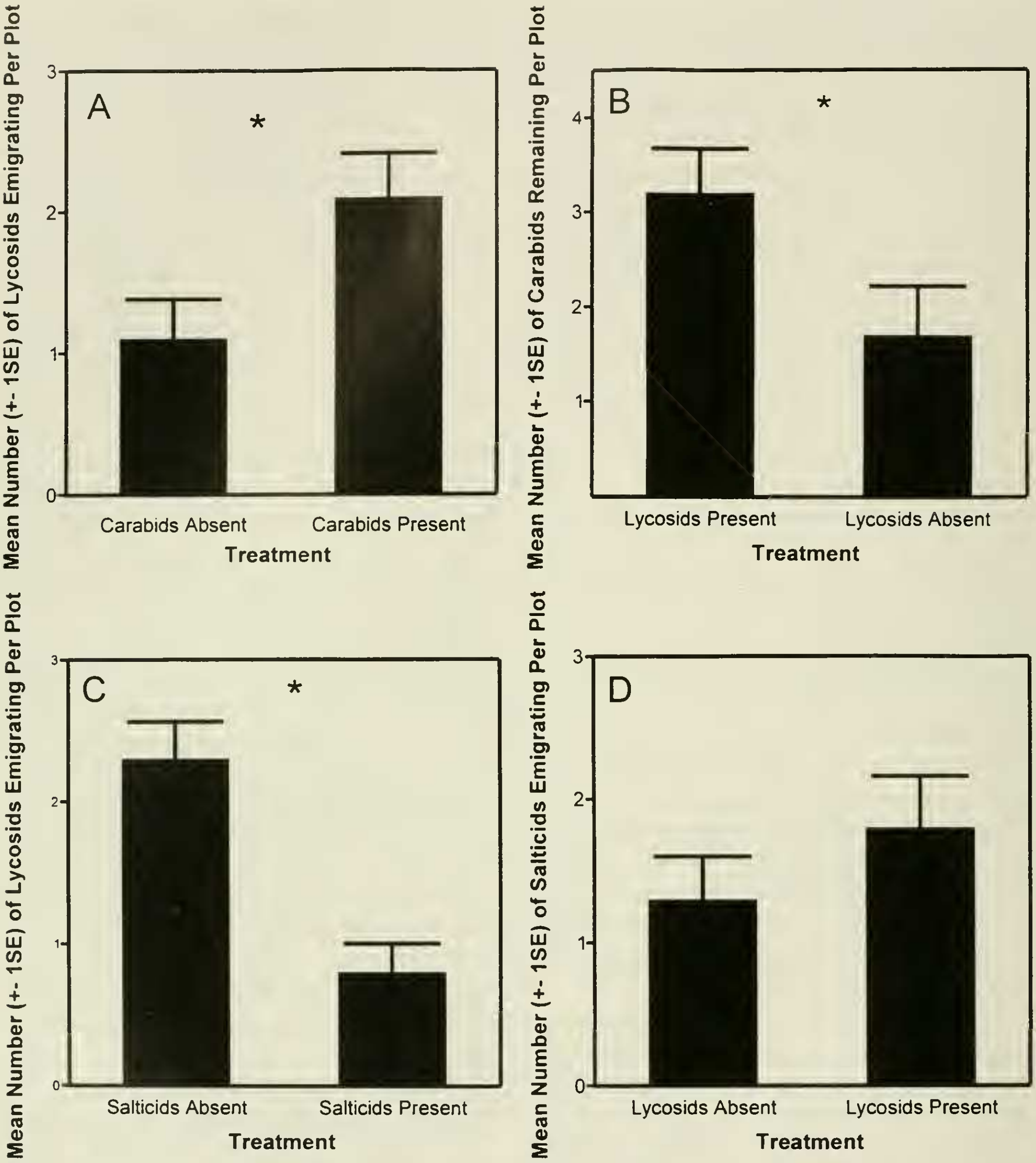

Fig. 2. A, Field experiment 1 comparing of mean number of lycosids (*Rabidosa* sp.) emigrating when carabid beetles were absent and present. B, Field experiment 1 comparing of number of carabids (*Harpalus* sp.) remaining in plots when lycosids were absent and present; N = 10 for each treatment group. C, Field experiment 2 comparing of the mean number of lycosids (*Rabidosa* sp.) emigrating when salticids are absent and present. D, Field experiment 2 comparing of the mean number of salticids emigrating when lycosids are absent and present, N = 10 for each treatment group. An asterisk (*) indicates statistical significance (Mann-Whitney U-test).

terns shown in this study indicate that intraguild predation is significant enough to alter this temporal use of habitat; small individuals are more active when predation risk is lower.

Some spiders are active both day and night (Uetz 1975, Hayes and Lockley 1990, Moring and Stewart 1994), although their activities typically peak during specific times of the day. Lycosids have well-developed sense organs for detecting vibrations, metatarsal and pretarsal slit sense organs for detection of vibrations on a substrate (Barth 1985), and trichobothria for detecting airborne vibrations (Lizote and Rovner 1988). These presumably enhance capture efficiency of prey at night. Researchers have usually attributed these peaks in activity to favorable environmental conditions (Riechert 1976, Kronk and Riechert 1979, Moring and Stewart 1994). We suggest that some activity peaks represent, in part, avoidance of intraguild predation and competition.

Our experiments do not definitively show that activity patterns are caused by these interactions. However, the ability of species to respond behaviorally to the presence of potential predators, competitors, or both, along with the observational data showing apparent temporal niche partitioning, indicate that these interactions are important. This temporal niche partitioning may in part explain why little competition has been demonstrated among spiders (Polis et al. 1989, Wise 1993) and may help explain the coexistence of the numerous predatory arthropods found in many terrestrial habitats. We predict that the activity patterns of these generalist predators are quite plastic, and species will adjust their temporal use of habitat to times when potential competition and predation are minimized.

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